Orientation of Carrion Beetles to Carrion: Random or Non-random?

PAUL P. SHUBECK[1]
ZOOLOGY DEPARTMENT, RUTGERS—THE STATE UNIVERSITY,
NEW BRUNSWICK, NEW JERSEY 08903

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Abstract: Carrion-baited ground cans were used to collect carrion beetles in Hutcheson Memorial Forest during the summers of 1961 through 1965. Fingernail polish colors were used to mark the elytra of the carrion beetles utilized in the orientation studies; the release-points of the recaptured individuals were thus identifiable. The rate of return to carrion by *Silpha noveboracensis* from distances of 5 to 75 meters was apparently due to random wandering and not because of orientation to carrion odors. The periphery of odor perception is about 1 meter from carrion when the movement of air is negligible. Carrion beetles were shown clearly to be attracted to carrion. However, the distance of this attraction is much less than what has generally been believed. In this study *S. noveboracensis* was fourteen times more apt to return to carrion than *Nicrophorus* sp. from 5 meters, whereas in a reported New England study these two species were about equally attracted to carrion from the same distance. A much greater overall return of Silphidae in the New England study was reported than is herein observed.

INTRODUCTION

A review of the literature on Silphidae (Coleoptera) gives a distinct impression that the beetles in this family have an extremely keen sense of detecting and locating carrion.

Fabre (1899), when writing about trapping the sexton beetle, observed, "To this carrion, ripened by the sun, the insect will not fail to hasten from the various points of the horizon, so accomplished is he in detecting such a delicacy."

Abbott (1927) said, "The olfactory powers of the Necrophori are certainly remarkable." He also stated, "Normal specimens of *Necrophorus tomentosus* detected meat which was slightly stale and almost certainly placed in situations far from their immediate habitat." In 1937, he spoke of "the ability of the

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[1] Present address: Biology Department, Montclair State College, Upper Montclair, New Jersey 07043.

adults [of necrophilous Coleoptera] to detect and follow the slightest odor of decaying flesh."

Dethier (1947) said, "The speed with which the insect is able to return to the source of an odor from distances in excess of 15 feet and the high percentage of returns from those liberated at this distance points to the existence of a klino-kinetic mechanism rather than truly random movement."

As recently as 1964 Lanham wrote, "These beetles fly in, apparently from considerable distances, guided by scent."

These studies were originally initiated with the goal of determining the maximum distance from which certain Silphidae would be capable of detecting and travelling to carrion bait. As the work progressed, however, it became increasingly clear that the real question was—Is orientation of carrion beetles to carrion random or is it non-random?

The research was conducted in the William L. Hutcheson Memorial Forest, which is located near East Millstone, Somerset Co., New Jersey. This forest has been relatively undisturbed during the past 260 or more years (Bard, 1952) and is one of the few mature stands of deciduous forest remaining in central New Jersey (Monk, 1957).

METHODS

The beetles were trapped in galvanized, one-gallon cans such as are discarded in large numbers at restaurants and cafeterias. Each can was buried with the open end level with the surface of the soil. To keep out the rain, the open end was covered with a piece of galvanized metal, one foot-square, supported so that there was a clearance of 2 to 4 inches between cover and can (Walker, 1957). This ground can was used in 1963 and 1964. During the summer of 1965 a one-half inch mesh screen cover was fitted to the top of the trapping can (Fig. 1). This served to prevent the loss of carrion, which had been occasionally removed, apparently by carnivorous mammals.

Walker (1957) and Jaques (1915) used fish as bait for the trapping of carrion beetles. Fabre (1899) scattered moles in his orchard for this purpose. Each trap in this study was baited with an uncooked chicken leg ("drum stick"). Chicken legs were used because they were always available, they were suitable attractants of carrion beetles, and they retained some attractant value for 10 or 12 days.

Fingernail polish colors were used to mark the elytra of the carrion beetles. By varying the color of the polish and the location of the markings, it was an easy task to designate the beetles which were to be released at the various points, and thus, to correlate the recaptured individuals with their release-points. A small amount of carbon dioxide from a portable tank was used to temporarily inactivate the beetles in order to mark them.

A total of 460 individuals of the species *Silpha noveboracensis* was marked and released at various distances from the collecting station in 1964. The

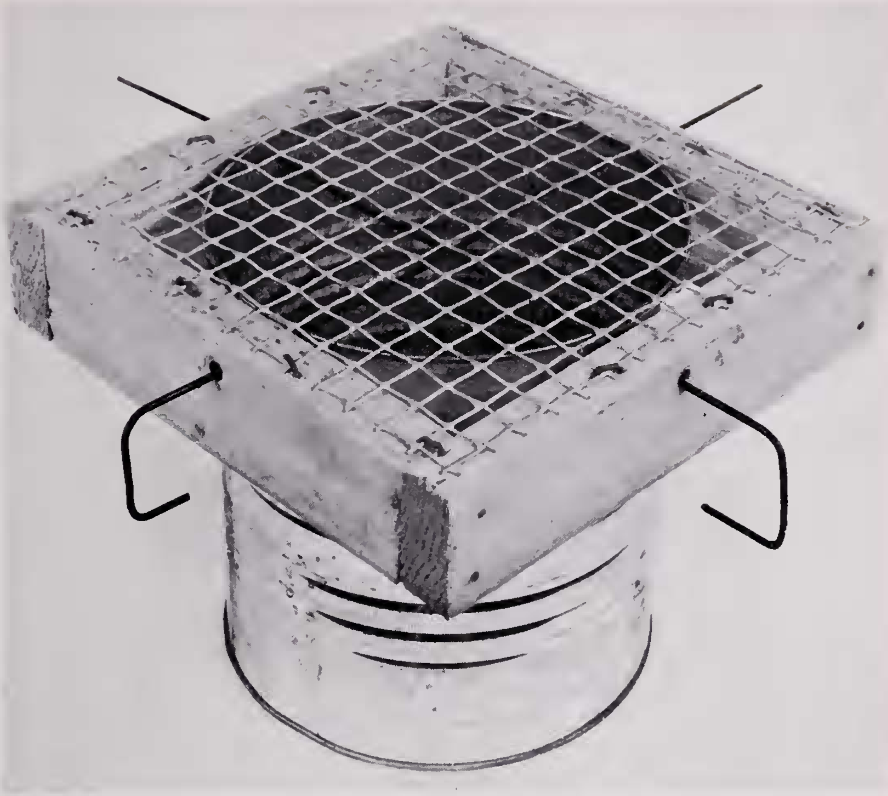

FIG. 1. Ground can with one-half inch wire screen cover to prevent loss of carrion (used in 1965).

station consisted of four ground cans baited with carrion. The individual cans were sunk at points north, east, south and west, each 5.8 meters distant from a central stake. An imaginary circle through the four cans was considered to be the trapping station or trapping circle. Fifty individuals were released east of the trapping circle at distances of 5, 15, 25, 50, 55, 60, 65, and 70 meters, and sixty individuals were released at 75 meters. This furthest release-point was chosen since there had been no return from this distance in a pilot study in 1963 when 76 individuals of this species had been marked and released. Inspection trips to the traps were undertaken every second day from 29 June to 19 July. This arrangement was necessary in order to ensure the capture for marking of a large number of beetles.

During the early part of the summer of 1965 this study was continued. Four new cans were sunk in the ground, similar to the arrangement of the previous year, but each can was situated exactly 5 meters from the central stake.

Twenty marked individuals were released at each 1 meter interval along a line extending from each can to the central stake. The central stake was included as a release-point; there were thus 17 release-points. A total of 80 beetles was released at 1 m, 80 each at 2 m, 3 m, 4 m, and 20 at the central stake. Thus, a total of 340 marked individuals was released. The marking and recapture work was conducted from 29 June to 8 July. Visits were made every second day to the collecting station during the first week and daily during the second week of the study.

During the summers of 1963 and 1964, 205 individuals of the taxon *Nicrophorus* sp. (*N. orbicollis* and *N. tomentosus*) were also marked and released. This taxon was not as abundant as was *Silpha noveboracensis*. As a result, the numbers of individuals released at each release-point were not uniform, and the number of release-points was less. Sixteen individuals were marked and released at 75 m, 30 at 50 m, 65 at 25 m, and 94 at 5 m.

RESULTS

The results of the marking and recapture study when 460 individuals of the species *Silpha noveboracensis* were released are given in Table 1. *S. noveboracensis* showed less than a 2% return from a distance of 75 m and only 28% when released 5 m from carrion. The rate of return from 75 m to 5 m increased linearly as the distance was reduced. These data seemed to suggest that the beetles were not very efficient in so far as orientation to specific carrion odors was concerned. Certainly, odor did not seem very effective in attracting this species at distances of 5 m or more.

Examination of the 1965 data on *Silpha noveboracensis* involving the release of these individuals at close intervals within 5 meters (Figs. 2 and 3) seems to indicate that only at 1 m distance was there a change in response to the carrion bait. At this distance there was a 45%, 50%, 45%, and 55% return at the north, east, south, and west cans respectively for an average return of 48.75%. The results at 2, 3, and 4 meters respectively never exceeded 19%. The mean number of beetles that returned from 2, 3, and 4

TABLE 1. Mark and recapture study of *Silpha noveboracensis*, 1964

Meters	Number Released	Number Returned	% Return
75	60	1	1.7
70	50	2	4
65	50	1	2
60	50	3	6
55	50	4	8
50	50	5	10
25	50	10	20
15	50	11	22
5	50	14	28

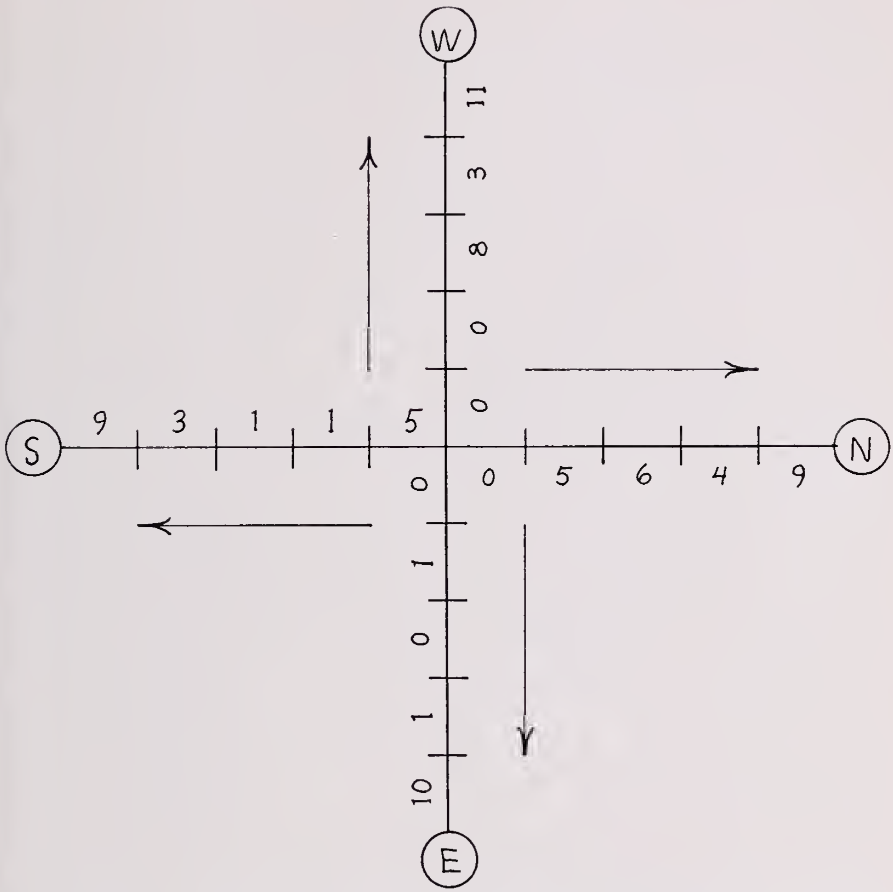

FIG. 2. Recaptures from distances of 1 to 5 meters. A total of 340 individuals of *Silpha noveboracensis* was marked and released for this study.

meters was 11. The number of beetles returning from 1 meter was 39. An average of $39 + 11 = 50$ was found. One would thus expect 25 of these beetles to return from 1 m and 25 from the average of 2, 3, and 4 m if one proceeds on the basis of the Null Hypothesis that there is no significant difference in ability to detect carrion at 1 m as compared with 2, 3, and 4 m.

$$X^2 = \frac{(39-25)^2}{25} + \frac{(11-25)^2}{25} = 15.68$$

Since the table of X^2 values shows a value of 3.84, with 1 degree of freedom, at the 5% level of significance, the Null Hypothesis must be rejected and thus, the ability to detect carrion at 1 meter as compared with 2, 3, and 4 meters is significantly higher.

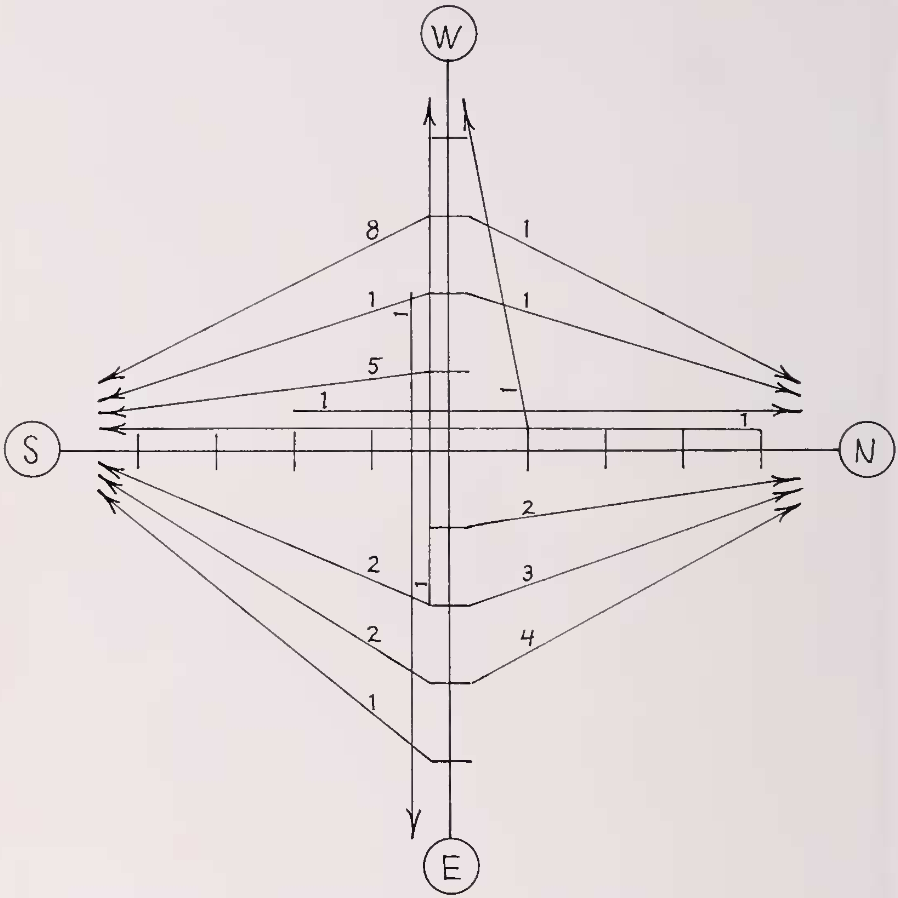

FIG. 3. Recaptures from distances of 5.1 to 9 meters. These results were obtained from the same sample of 340 individuals of *Silpha noveboracensis* mentioned in Fig. 2.

In evaluating these returns, the question arose—was the return random or was positive orientation to carrion involved? One analysis of this question can be made by examining the number of beetles released at 2, 3, and 4 meters that was trapped at the closest cans (from point of release) as compared with the number of beetles released at the same distances that was trapped at the other more distant cans. A total of 33 marked beetles from 240 individuals that had been released at 2, 3, and 4 meters was trapped at the closest cans (Fig. 2). An equal number of marked beetles, from the same 240 individuals, was also taken at the other, more distant cans (Fig. 3). Since the ratio was exactly 1:1 it would seem that this is random return, and not direct orientation, from distances of 2, 3, and 4 meters.

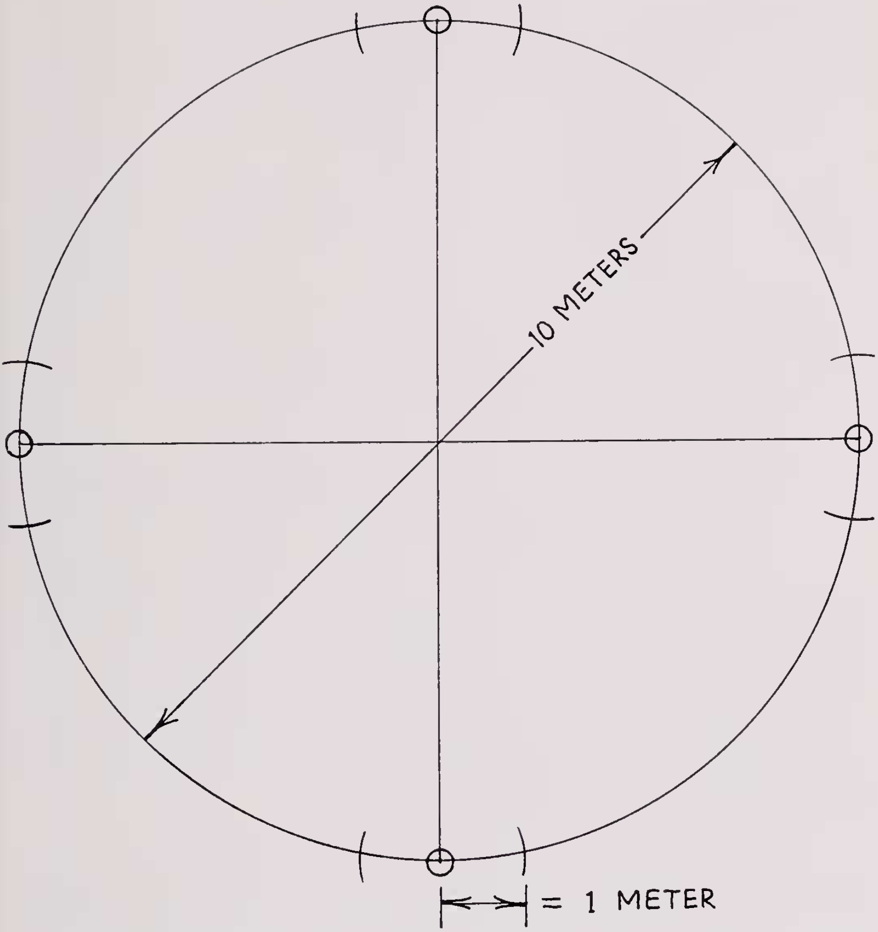

FIG. 4. Determination of that portion of the trapping circle where crossing beetles can come under the influence of carrion odor. $C = \pi D$, $C = 3.14 \times 10$, $C = 31.4$ meters; 2 meters $\times$ 4 cans $=$ 8 meters; $\frac{8}{31.4} = 25\%$.

A second approach to the question of random orientation was pursued. Since it is shown that there is a significant difference in ability to detect carrion at 1 meter, a circle can be constructed whose arc goes through the four carrion-baited cans and show that beetles crossing at portions of this arc can detect carrion and be trapped.

To determine that portion of the circle where carrion odor is significant the arcs are marked 1 meter on each side from the center of each of the four cans (Fig. 4). Hence, through 8 meters of the total 31.4 meters (or 25.5%) of the arc, moving carrion beetles can be influenced by carrion odor.

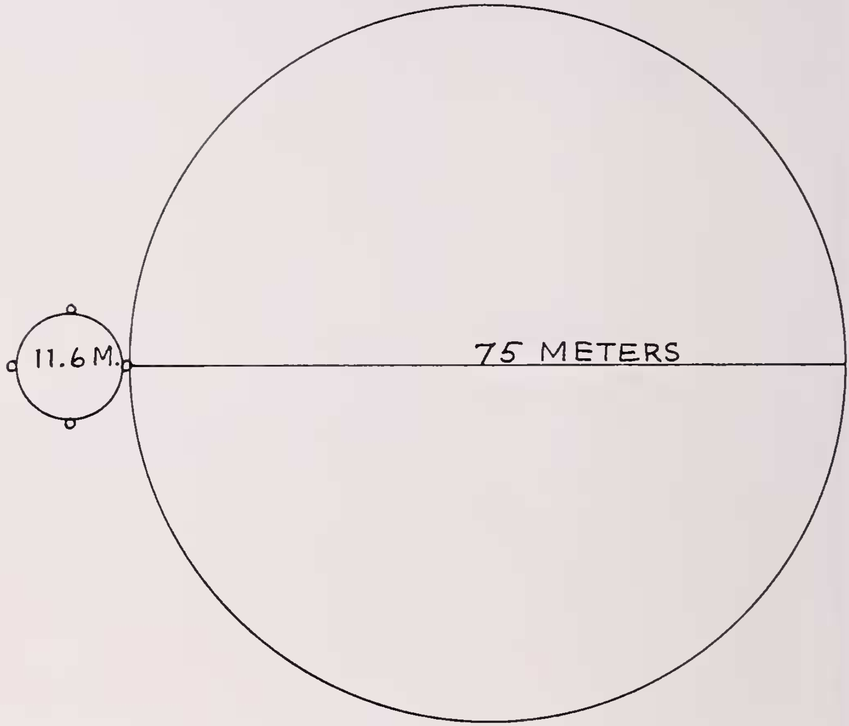

FIG. 5. Determination of the theoretical probability of recapture from 75 meters. $\frac{\pi \text{ D (trapping circle)}}{\pi \text{ D (release-point circle)}}$ $(\text{K}) = \text{P}$; $\frac{\pi\ 11.6}{\pi\ 75}$ $(.33) = \text{P}$; $.05 = \text{P}$.

Proceeding on the basis of the Null Hypothesis: If beetles are released within a circle at 2, 3, 4, and 5 meters from carrion-baited cans, they will cross the arc of the circle in a random fashion so that 25.5% of the 260 individuals will cross the circle within 1 meter of any can and be under the influence of carrion odor, whereas 74.5% of the 260 individuals will cross the circle at distances greater than 1 meter from any can and will not be trapped; the computed X^2 was found to be 0.506.

$$X^2 = \frac{(71-66)^2}{66} + \frac{(189-194)^2}{194} = 0.506$$

Since the table of X^2 values shows a value of 3.84, with 1 degree of freedom, at the 5% level of significance, the Null Hypothesis is accepted. This is further evidence that return from 2, 3, 4, and 5 meters is random.

In a paper on movement of Malayan rats Harrison (1958) showed that movement toward a predetermined home range circle was random. He stated that . . . "Since the search is assumed to be random, the rat may be expected

TABLE 2. Actual return compared with theoretical return of 410 individuals of *Silpha noveboracensis.*

Release-point	Actual % Return	Theoretical Probability	±
15 Meters	22.0%	25.8%	+ 3.8%
25 Meters	20.0%	15.4%	– 4.6%
50 Meters	10.0%	7.7%	– 2.3%
55 Meters	8.0%	7.0%	– 1.0%
60 Meters	6.0%	6.4%	+ 0.4%
65 Meters	2.0%	6.0%	+ 4.0%
70 Meters	4.0%	5.4%	+ 1.4%
75 Meters	1.7%	5.0%	+ 3.3%
			± 2.6%

to approach the home circle from any direction, and the important dimension is not the angle subtended by the home range at the point of release (as might be expected) but the circumference of the range compared with the circumference of the circle at that distance from the point of release."

The probability of its discovery is, therefore, π D of home circle / π D of release-point circle. Since the probability of recapture (based on past experience) must be taken into consideration this figure is used as a correction factor (K). We used Harrison's method as evidence to support our hypothesis that the return of *Silpha noveboracensis*, from 5 to 75 meters, in our 1964 study was random return. Our correction factor, based on recapture experience (112/340), was 33.5%.

Figure 5 shows how the probability was derived for the release-point at 75 meters. Since the diameter of the circle at the nearest release-point is less than that of the "trapping circle," the probability of random return was not determined at 5 meters. Probabilities were determined, however, for all other release-points from 15 meters to 75 meters (Table 2).

When the probabilities were plotted against the line showing the actual return, the results were very similar (Fig. 6). The correlation between the theoretical line for random return and the actual line seems to be very good.

The goodness of fit (Dixon & Massey, 1957) of the actual return as it compared with Harrison's theoretical probability for random return was computed using the Chi Square Statistic. The observed figures were derived from the actual return (Table 1) and the expected figures were derived from the theoretical probabilities (Table 2).

$$X^2 = \frac{(11-12.9)^2}{12.9} + \frac{(10-7.7)^2}{7.7} + \frac{(5-3.9)^2}{3.9} + \frac{(4-3.5)^2}{3.5} +$$

$$\frac{(3-3.2)^2}{3.2} + \frac{(1-3)^2}{3} + \frac{(2-2.7)^2}{2.7} + \frac{(1-2.5)^2}{2.5} = 3.73$$

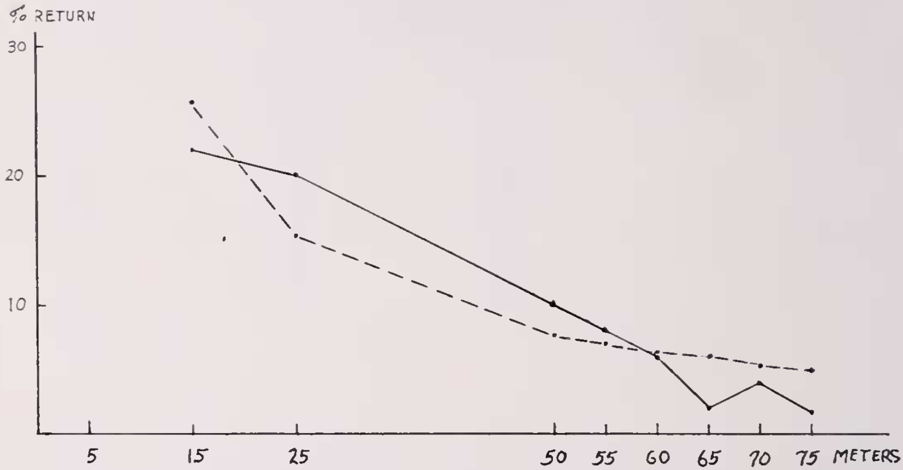

FIG. 6. The solid line shows the actual rate of return from 410 individuals of the species *Silpha noveboracensis*. The dashed-line shows the theoretical line for random return.

Since the computed X^2 is 3.73 and the theoretical X^2, with 7 degrees of freedom at the 5% level of significance, is 14.07, there seems to be a very good fit to Harrison's model for random return. Thus, with 95% probability, the return of *Silpha noveboracensis* to carrion from distances of 5 meters to 75 meters is a random return.

The results of the mark-recapture study of 205 individuals of *Nicrophorus* sp. showed a much lower rate of return than that of *Silpha noveboracensis* (Fig. 7). There was but a 7.1% return from 25 meters in 1963 and a mere 2.1% return from 5 meters in 1964.

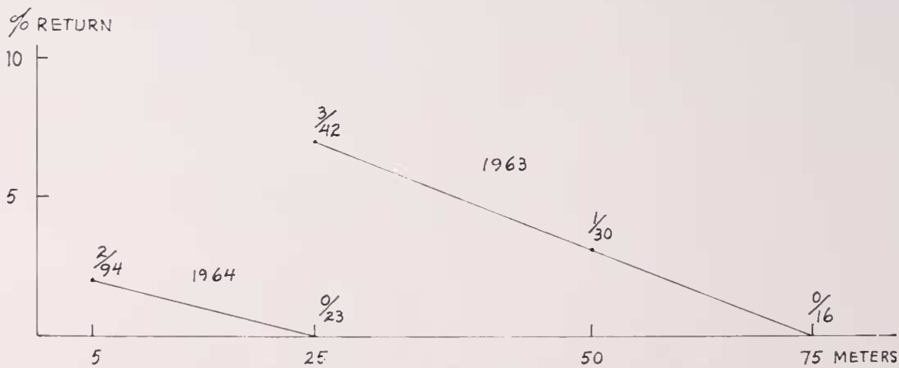

FIG. 7. Individuals of *Nicrophorus* sp. (*N. orbicollis* and *N. tomentosus*) marked and recaptured during 1963 and 1964. The denominator indicates the number marked and released and the numerator indicates the number recaptured.

In general, it seems clear that when wind movement is negligible, as is the case in Hutcheson Memorial Forest (Bruce Wales, graduate student doing research on climatology of Hutcheson Memorial Forest; personal communication), the Silphidae must be very close to carrion in order to detect it.

DISCUSSION

The results of these studies seem to indicate quite clearly that in so far as Silphidae in Hutcheson Memorial Forest are concerned, they are not nearly as efficient in detecting carrion as other populations of Silphidae have been reported to be by other investigators. On the basis of the results obtained in 1964 and 1965, using 800 marked individuals, it seems evident that:

There is a linear relationship in the distance at release and rate of return to carrion by *Silpha noveboracensis* when released at distances from 5 to 75 meters. This is apparently due to random wandering and not because of orientation to carrion odors.

There is a significant increase in ability to return to carrion below 2 meters. The periphery of odor perception seems to be about 1 meter from carrion. It is interesting to note that when working in the forest with carrion beetles, I can detect the presence of carrion at about 25 meters.

The results of the mark-recapture study of *Nicrophorus* sp. were different from the above. The 205 individuals (*N. orbicollis* and *N. tomentosus*) showed a much lower rate of return to carrion. These data seem to indicate random wandering to carrion and possibly a lower rate of activity since both at 25 meters and 5 meters *Nicrophorus* sp. had a much lower rate of return to carrion than *Silpha noveboracensis* (Table 3).

The above results are very different from those obtained by Dethier (1947) in a northern New England conifer forest. I note that the *Nicrophorus* sp. used by Dethier included *N. tomentosus* and *N. vespilloides*. The species *N. tomentosus* was common to both studies.

Two striking observations are evident when comparing these studies:

In the Hutcheson Memorial Forest study, *Silpha noveboracensis* was fourteen times more apt to return to carrion than *Nicrophorus* sp. from 5 meters, whereas in the New England study these two species were about equally attracted to carrion from the same distance.

Table 3. Comparison of orientation results in two different forests.

	New England Conifer Forest (Minimum of 15 Feet)		Hutcheson Memorial Forest (5 meters)	
	number released	percent returned	number released	percent returned
Nicrophorus sp.	70	87.5%	94	2%
S. noveboracensis	20	85.0%	50	28%

In the New England study there was a much greater overall return of Silphidae than that observed in the New Jersey study.

It is possible that this discrepancy is due to the fact that there is very little movement of air in Hutcheson Memorial Forest (Bruce Wales, personal communication). The wind may have played an important part in the high rate of return in Dethier's work. Haskell (1966), in fact, states that . . . "while Dethier (1947) ascribed carcass finding in four species of carrion beetle to a klino-kinetic mechanism, his description of the process fits better the idea of odour released anemotaxis."

It is interesting, too, to note that the results that Abbott (1927) obtained relating to the olfactory threshold of the Nicrophori differed so much from those obtained by him in a prior, unpublished study to which he referred. It is possible that different populations of Silphidae develop different patterns of behavior.

One other reason that could possibly explain the high rate of return in Dethier's work is that, for bait, he suspended exposed red squirrel carcasses five feet above the ground. Our carrion-baited can openings, on the other hand, were at the level of the soil surface. It is possible that the surface friction of the soil surface on the air (Geiger, 1965) reduced the movement of air (and odor) directly above the ground which resulted in a lower rate of return in our studies. Since animal carrion normally lies on the ground, it is possible that our results are more realistic.

There is no question but that the carrion-baited cans do attract carrion beetles. In a previous study in Hutcheson Memorial Forest conducted in 1961 and 1963 (Shubeck, 1967), the attraction of carrion bettles to several baits was noted. There was a total of 36 collecting days during that study. Since there were three carrion-baited cans in the trapping circle, a total of 108 can collections were made. A total of 781 Silphidae was collected in these cans. There was thus a 7.2 average for each can collection during the two summers of study. Since each of three replicates in the trapping circle included cans baited with carrion, corn meal, potato, and an empty "control," there were also 108 can collections for corn meal-baited cans, a like number for potato-baited cans, and a like number of collections for empty cans. Not one carrion beetle was ever found in any of these cans. The fact that carrion beetles are attracted to carrion is quite clear. The studies discussed in this paper, however, seem to indicate quite strongly that the distance of this attraction is much less than generally believed.

I intend to continue orientation studies on carrion beetles in Hutcheson Memorial Forest and in other habitats. Experiments will be conducted to (1) demonstrate the nature of the orientation under windy conditions, determining whether it is purely chemotropotactic or if it involves anemotaxis, (2) determine the exact distance, in centimeters, from which the majority of released beetles will return to carrion, and (3) determine the radii of active spaces of decomposition odors in Silphidae in different environments.

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